Partitioning colony size variation into growth and partial mortality

Joshua S. Madin[1], Andrew H. Baird[2], Marissa L. Baskett[3], Sean R. Connolly[2,4], Maria A. Dornelas[5]

[1]Hawai'i Institute of Marine Biology, University of Hawai'i at Mānoa, Kaneohe, Hawai'i, USA
[2]ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville QLD 4811, Australia
[3]Department of Environmental Science and Policy, University of California, Davis, California 95616
[4]School of Marine and Tropical Biology, James Cook University, Townsville QLD 4811, Australia
[5]Centre for Biological Diversity, Scottish Oceans Institute, University of St. Andrews, KY16 9TH, Scotland, UK
*Corresponding author: Joshua Madin, jmadin@hawaii.edu

Abstract

Body size is a trait that broadly influences the demography and ecology of organisms. In unitary organisms, body size tends to increase with age. In modular organisms, body size can either increase or decrease with age, with size changes being the net difference between modules added through growth and modules lost through partial mortality. Rates of colony extension are independent of body size but net growth is allometric, suggesting a significant role of size-dependent mortality. In this study, we develop a generalisable model of partitioned growth and partial mortality and apply it to data from 11 species of reef building coral. We show that corals generally grow at constant radial increments that are size independent, and that partial mortality acts more strongly on small colonies. We also show a clear life history trade-off between growth and partial mortality that is governed by growth form. This decomposition of net growth can provide mechanistic insights into the relative demographic effects of the intrinsic factors (e.g., acquisition of food and life history strategy) that tend to affect growth and extrinsic factors (e.g., physical damage, and predation) that tend to affect mortality.

Key words

35 Body size, growth rate, colonial organism, partial mortality, life history trade-off, reef coral,
36 demography

1. Introduction

Body size is a fundamental organismal trait [1], which determines a range of physiological, demographic and ecological possibilities and outcomes [2]. For example, large bodied organisms have lower per-mass metabolic rates than small bodied organisms [3]; population densities of large species are expected to be lower than those of smaller ones because of their higher total metabolic demands [4]; and declines in average body size can foreshadow population declines [5]. An organism's ability to increase body size is its growth. For unitary organisms, growth is the only rate required to determine body size because they generally do not shrink, although losses in biomass are possible from decreased body condition. However, modular organisms can shrink, because modules can die without killing the whole organism (hereafter termed "partial mortality"). For example, herbivory or mechanical damage to such organisms can more than outpace growth and accretion rates [6,7]. For this reason, a mechanistic understanding of growth in modular organisms requires that the two processes of growth and partial mortality be estimated separately. Here, we use scleractinian reef building coral colonies to build a model that separates the intrinsic capacity to increase in size from the processes that act to reduce it.

We use scleractinian corals because the processes that add or reduce body size are well understood, with the addition of modules by asexual reproduction counteracted by the loss of modules through partial mortality [6]. If we were only interested in net change in body size, the effects of these counteracting processes could be considered only in the aggregate. For instance, demographic modelling is typically concerned with net changes in colony size through time and less-so with how these changes come about [8,9]. For corals, net growth tends to be allometric [10]. However, annual rates of linear extension in the absence of significant partial mortality (e.g., increasing branch length or colony radius) tend to be constant and independent of colony size [11,12]. We hypothesise that these apparently conflicting findings can be resolved by separating the effects of partial mortality from the ability to grow.

To do so, we developed a generalisable approach that separates change in colony size into its potential growth and partial mortality components. Using annual growth measurements across 11 reef-building coral species, we then test the hypotheses that 1) linear extension is constant but 2) partial mortality is size dependent. Finally, we test for a relationship between

potential growth and partial morality that may represent a fundamental life history trade-off for reef corals.

2. Material and Methods

We estimated yearly changes in planar area for 11 species of scleractinian corals. We tagged 30 colonies of each species, which were distributed along a 500 m by 10 m band of reef crest at Trimodal reef, between South and Palfrey islands (14.6998398 S, 145.4486748 E), Lizard Island, Australia. Each tagged colony was photographed from above with a two-dimensional scale plate placed level with the surface of the colony (Fig. S1). The angle of the camera was horizontal, and the distance from the colony was such that the entire colony was visible in the photograph. Tagged colonies were photographed yearly in November from 2009 to 2013. The images were corrected for barrel distortion, and the scale and outline of each colony were digitized in ImageJ to estimate colony size (Fig. S1). Every year, dead or missing colonies were replaced in order to maintain approximately 30 colonies per species. We did this to ensure that size-selective mortality would not progressively reduce the range of colony sizes available to characterize size-dependent growth. To minimize the effect of observation error, colonies were photographed twice to three times independently every year. All photographs were digitized twice independently and estimates of area were averaged.

To test the constant rate of linear growth hypothesis, we first calculated, for each colony, the radius of a hypothetical circular colony with the same planar area as the corresponding real colony. We then calculated the yearly change in radii for each individual colony that survived over a given time interval and, for a given species, assumed that those with the greatest positive radial change per year were those suffering the least partial mortality (i.e., colonies can grow at least at this rate). We used quantile regression models to capture the extreme upper bound (95% quantile) of relationships between annual added radius and the planar area of a colony for each species separately. Because some colonies were measured over multiple years, we first used linear quantile mixed effect models with colony ID as a random intercept; using “lqmm” [13] in the statistical software, R [14]. Variance of the random effect was consistently much lower than differences among model estimates—suggesting that colony growth of individuals could be treated independently from year to year—and so we removed the random effect and used basic quantile regression instead; using the “rq” function [15]. We tested if the slope of the upper quantile as a function of colony planar area was statistically

105 indistinguishable from zero (i.e., size independent). Given 11 species comparisons, we
106 applied a Bonferroni correction to the p-value. For a colony of planar area x at time t, yearly
107 potential increase in colony area (growth) g from radial growth r_s for each species s was
108 given by:

109 $$g(x, r_s) = \pi \left(\sqrt{\frac{x}{\pi}} + r_s \right)^2, \qquad \text{Eq. 1}$$

110 where the square-root term is the initial radius of a circular colony of planar area x. To test if
111 our assumption of colony circularity affected the results, we calculated the circularity of
112 colonies as the ratio of colony digitized outline lengths and the perimeter of a circle with the
113 same planar area. (Thus, a perfectly circular colony would have a ratio of 1.) Colony
114 residuals of the quantile regression models for each species (above) were plotted against
115 colony circularity values, and Spearman's correlations were calculated to quantify the
116 strength of associations.
117
118 Partial mortality operates over the range between maximum potential growth (i.e., no partial
119 mortality) and whole colony death (i.e., partial mortality that is equal to colony size). We
120 estimated partial mortality p as the proportion of area lost across years following potential
121 growth, which is one minus the area remaining, given by:

122 $$p(x, y, r_s) = 1 - \frac{y}{g(x, r_s)}, \qquad \text{Eq. 2}$$

123 where y is area at time t+1. To test if colony size affected the proportion partial mortality, we
124 used linear models mixed effects models for species, where partial mortality was logit
125 transformed and colony ID was the random intercept; using "lmer" [16]. As for quantile
126 regressions, the random effect accounting for the same individuals measured in multiple
127 years explained little variation and was removed.
128
129 Finally, we calculated the combined annual growth probability f for each study species s by
130 combining yearly potential growth (Eq. 1) and partial mortality (Eq. 2) probabilities based on
131 colony size. We used the normal density function to model the probability of annual growth
132 to size y given a starting size x and, for species s, the yearly added radius r_s and the slope m_s,
133 intercept c_s and error σ_s parameters for partial mortality. The growth component was logit
134 transformed before calculating the probability of attaining size y given partial mortality, and
135 the result back-transformed using the inverse logit (Eq. 3).

136 $$f(x, y, r_s, m_s, c_s, \sigma_s) = logit^{-1}\left(\frac{1}{\sqrt{2\pi}\,\sigma_s} e^{-\left(\frac{[logit(p(x,y,r_s))-m_s x+c_s]^2}{2\,{\sigma_s}^2}\right)}\right).$$ Eq. 3

137

138 **3. Results**

139

140 The maximum potential growth (measured as radial extension) of coral colonies did not
141 change significantly with colony size (Fig. S2, Table S1). Given general support for constant
142 radial growth across species, we present intercept-only model estimates in Table 1, which
143 gives the rank order of potential yearly extension. Potential growth rate was greatest in the
144 tabular species (*A. hyacynthus* and *A. cytherea*) that were estimated to add between 7-10 cm
145 radially each year in the absence of partial mortality. Potential growth was lowest for the
146 massive species (*Goniastrea retiformis* and *G. pectinata*) at between 1-2 cm per year. No
147 strong or consistent associations were found between circularity and growth model residuals
148 (Spearman rho ranging between -0.191 and 0.368), suggesting that departure from circularity
149 had a small effect on the extension rate estimates (Fig. S3).

150

151 Generally, yearly partial mortality decreased with colony size (Table 2, Fig. S4); although,
152 the relationships were not significant for *A. nasuta* and *A. millepora*. The life history trade-
153 off between growth and partial mortality is presented in Figure 1. The combined growth
154 model (Eq. 3) based on growth and partial mortality parameter estimates from Tables 1 and 2
155 is presented in Fig. 2.

156

157 **4. Discussion**

158

159 In this study, we developed a growth model that separates maximum potential growth from
160 partial mortality. In doing so, we show that reef corals growth is generally consistent with
161 constant annual radial increments, as previously suggested [11,17]. Change in the perimeter
162 to area ratio as colonies grow causes a curvilinear change in maximum potential growth (Fig.
163 2, solid upper curves), with the curve particularly evident for small sizes. This curve implies
164 that size increase (in the absence of partial mortality) deviates from allometric growth.
165 However, net growth—that includes both growth and partial mortality—tends to be
166 allometric [10]. This inconsistency occurs because partial mortality is size dependent and acts

to suppress the proportionally large size gains when colonies are small (Fig. S3), which suppresses the upwards inflection of potential growth among smaller colonies.

Growth and partial mortality trade-off strongly, where faster growing species have higher rates of partial mortality than slower growing species (Fig. 1). The position of species along the trade-off dimension was determined by growth form (shown as silhouettes in Fig. 1), showing a clear pattern from slow growing, mechanically robust to fast growing delicate colony shapes [18,19]. The trade-off also helps explain similarities in net growth when there are substantial differences in radial growth (Fig. 2). The consistency in patterns in potential growth and partial mortality across the 11 species in this study suggests that our findings are robust and should generalise to other species based on morphological traits.

One implication of this result is that estimates of growth based on estimates from large colonies will underestimate growth of recruits and small colonies, and hence the potential reef recovery rates following a disturbance. As a consequence, growth in very small colonies can be disproportionately fast relative to their size, especially in the absence of partial mortality. The potential to increase colony area when small by over an order of magnitude in one year (Fig. 2, solid upper curve) is the mechanism that underlies the efficacy of micro-fragmenting (the chopping up of large colonies to increase overall areal growth rate) for reef restoration as it allows rapid generation of a large number of colonies for outplanting [20].

Separating growth and partial mortality is important for modelling the dynamics of modular organisms, because the two components are influenced by different biological, ecological and environmental processes. Growth is influenced by access to resources and life history strategy; that is, the pattern of allocation of energy among reproduction, growth, maintenance and repair [21]. In turn, each of these processes are influenced by the environment and interactions with other organisms. On the other hand, partial mortality of colonies is more influenced by external processes, such as competition, predation and damage, for example, from waves [6]. Separating the intrinsic and extrinsic processes that lead to net growth will also allow for improved, mechanistic predictions of the ecological and evolutionary consequences of environmental changes. For example, reduced seawater pH will affect carbonate availability for building skeletons, and therefore might result in a trade-off between growth rate and skeletal density. On one end of this trade-off, maintaining a given growth rate at the cost of lower skeletal density might increase the potential for partial and whole-

colony mortality. At the other end of this trade-off, maintaining skeletal density might result in slower growth and the consequent reduction in reproductive output [22] and competitive capacity [23]. Modelling mechanistic trade-offs such these at the population level to inform expectations under future environmental change requires the separation of growth into its constituent parts.

Acknowledgements

We are grateful to Mizue Hissano, Lo¨ic Thibault, Maddeline Emms, Miguel Barbosa, Erin Graham, Dominique McGowan, Vivian Cumbo, Emily Howels, Shane Blowes, Marcela Diaz and Mariana Alvarez Noriega for help in collecting the data. We are also grateful to the staff at Lizard Island Research Station, in particular Anne Hoggett and Lyle Vail.

Funding

We thank the Australian Research Council for fellowship and research support. MD is funded by a Leverhulme Fellowship and by the John Templeton Foundation grant #60501.

Figure captions

Figure 1. The association between yearly extension (added radius) and proportion partial mortality for the 11 study species. Points are shortened versions of species names. Proportion partial mortality was estimated for a colony size of 0.01 m^2 (equivalent to a 10 by 10 cm colony) for each species. Silhouettes of species growth forms are superimposed.

Figure 2. Planar area of colonies at t+1 as a function of the area at time t for the 11 study species. Points show the field data. The dashed line in the stasis line. The solid line is maximum potential growth (i.e., added radial growth and no partial mortality). Shading represents estimated probability of colony size at t+1 given size at t (red is the band of highest probability).

References

1. Peters RH. 1983 *The Ecological Implications of Body Size*. Cambridge University Press.
2. Marquet PA, Quiñones RA, Abades S, Labra F, Tognelli M, Arim M, Rivadeneira M. 2005 Scaling and power-laws in ecological systems. *Journal of Experimental Biology* **208**, 1749–1769.
3. Kleiber M. 1932 Body size and metabolism. *Hilgardia* **6**, 315–351.
4. Damuth J. 1981 Population-density and body size in mammals. *Nature* **290**, 699-700.
5. Clements CF, Ozgul A. 2016 Including trait-based early warning signals helps predict population collapse. *Nature Communications* **7**, 10984.
6. Buddemeier RW, Kinzie RA. 1976 Coral Growth. Oceanogr. *Mar. Biol. Ann. Rev.* **14**, 183-225.
7. Maron JL, Crone E. 2006 Herbivory: effects on plant abundance, distribution and population growth. *Proc Royal Soc London B* **273**, 2575-2584.
8. Hughes TP, Jackson JBC. 1980 Do Corals Lie About Their Age? Some Demographic Consequences of Partial Mortality, Fission, and Fusion. *Science* **4457**, 713-715.
9. Madin JS, Hughes TP, Connolly SR. 2012 Calcification, storm damage and population resilience of tabular corals under climate change. *PLoS ONE* **10**, e46637.
10. Dornelas M, Madin JS, Baird A, Connolly S. 2017 Allometric growth in reef-building corals. *Proceeding of the Royal Society London B* **284**, 20170053.
11. Connell JH. 1973 Population ecology of reefbuilding corals. In *Biology and geology of coral reefs* (eds OA Jones, R Endean), pp. 205–245. New York, NY: Academic Press.
12. Hughes TP, Jackson JBC. 1985 Population Dynamics and Life Histories of Foliaceous Corals. *Ecological Monographs* **55**, 141–166.
13. Geraci M. 2014 Linear Quantile Mixed Models: The lqmm Package for Laplace Quantile Regression. *Journal of Statistical Software* **57**, 1-29.
14. R Core Team. 2018 R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.
15. Koenker R. 2019 quantreg: Quantile Regression. R package version 5.40. https://CRAN.R-project.org/package=quantreg
16. Bates D, Maechler M, Bolker B, Walker S. 2015 Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software **67**, 1-48.
17. Pratchett M, Anderson K, Hoogenboom M, Widman E, Baird A, Pandolfi J, Edmunds P, Lough J. 2015 Spatial, Temporal and Taxonomic Variation in Coral Growth—

Implications for the Structure and Function of Coral Reef Ecosystems. In: Hughes R., Hughes D., Smith I., Dale A. (eds) *Oceanography and Marine Biology*. CRC Press, pp 215–296.

18. Madin JS. 2005 Mechanical limitations of reef corals during hydrodynamic disturbances. *Coral Reefs* **24**, 630–635.
19. Zawada KJA, Dornelas M, Madin JS. 2019 Quantifying coral morphology. *Coral Reefs* **38**, 1281-1292.
20. Forsman ZH, Page CA, Toonen RJ, Vaughan D. 2015 Growing coral larger and faster: micro-colony-fusion as a strategy for accelerating coral cover. *PeerJ* **3**, e1313.
21. Kooijman SALM. 2010 *Dynamic energy budget theory for metabolic organisation*. Cambridge, UK: Cambridge University Press.
22. Pianka ER, Parker WS. 1975 Age-Specific Reproductive Tactics. *The American Naturalist* **109**, 453–464.
23. Lang J, Chornesky E. 1990. Competition between scleractinian reef corals: a review of mechanisms and effects. In Z. Dubinsky, ed. *Ecosystems of the world*. Pages 209-252. Elsevier, Amsterdam.

280 **Table 1**. Regression intercept estimates for upper 95% quantiles of added radius for the 11
281 species of reef building coral, ranked from highest to lowest. Estimates are potential radial
282 growth r_s for species in metres per year.
283

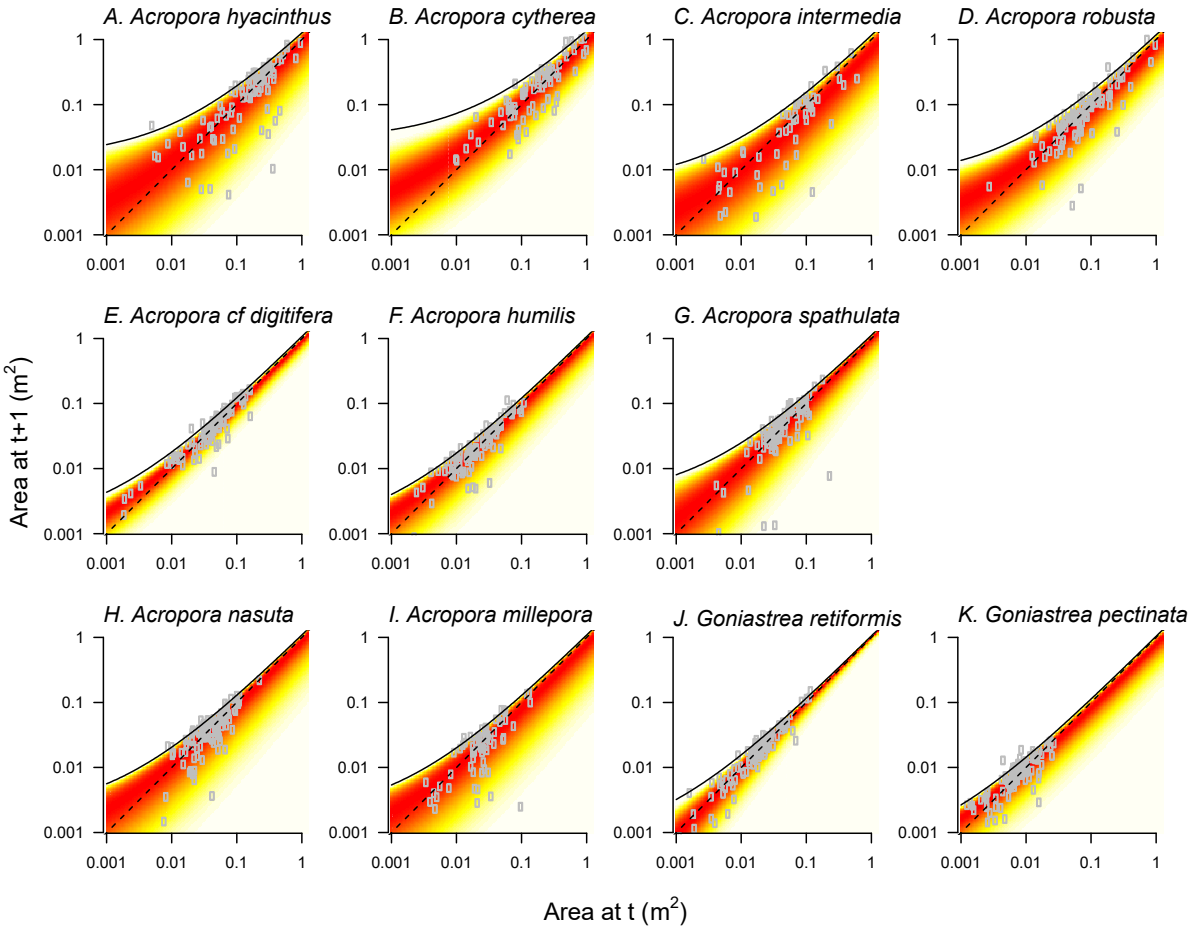
Species, *s*	**Growth form**	**Estimated r_s (my^{-1})**	**Std. error**	**t value**	**Pr(>|t|)**
Acropora cytherea	Tabular	0.096	0.018	5.353	<0.001
Acropora hyacinthus	Tabular	0.070	0.006	12.321	<0.001
Acropora robusta	Arborescent	0.049	0.010	4.874	<0.001
Acropora intermedia	Arborescent	0.044	0.011	4.151	<0.001
Acropora spathulata	Corymbose	0.033	0.004	7.615	<0.001
Acropora nasuta	Corymbose	0.024	0.002	10.576	<0.001
Acropora millepora	Corymbose	0.024	0.003	7.323	<0.001
Acropora cf digitifera	Digitate	0.019	0.004	4.436	<0.001
Acropora humilis	Digitate	0.018	0.002	7.270	<0.001
Goniastrea retiformis	Massive	0.014	0.002	6.671	<0.001
Goniastrea pectinata	Massive	0.014	0.004	3.376	<0.001

284

Table 2. Regression estimates for linear models of logit partial mortality as a function of colony size for the 11 species of reef building coral. § denotes species without a significant slope with a Bonferroni correction alpha of 0.0045. σ_s is residual standard deviation for species.

Species, *s*	**Parameter**	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**	**σ_s**
Acropora hyacinthus	*c* (intercept)	-0.963	0.3	-3.213	0.002	1.397
	m (slope)	-1.177	0.311	-3.786	<0.001	
Acropora cytherea	*c*	-0.276	0.205	-1.35	0.181	0.851
	m	-1.054	0.222	-4.753	<0.001	
Acropora intermedia	*c*	-0.468	0.408	-1.146	0.258	1.177
	m	-1.042	0.283	-3.68	0.001	
Acropora robusta	*c*	-0.518	0.254	-2.037	0.044	0.899
	m	-1.172	0.216	-5.433	<0.001	
Acropora cf digitifera	*c*	-1.646	0.252	-6.541	<0.001	0.656
	m	-0.939	0.174	-5.402	<0.001	
Acropora humilis	*c*	-1.394	0.293	-4.749	<0.001	0.589
	m	-1.134	0.172	-6.596	<0.001	
Acropora spathulata	*c*	-1.847	0.596	-3.099	0.003	1.213
	m	-1.236	0.422	-2.926	0.004	
Acropora nasuta	*c*	-1.347	0.631	-2.135	0.035	1.268
	m	-0.868	0.441	-1.966	0.052 §	
Acropora millepora	*c*	-0.837	0.836	-1.001	0.320	1.410
	m	-0.512	0.509	-1.005	0.319 §	
Goniastrea retiformis	*c*	-2.927	0.313	-9.362	<0.001	0.685
	m	-1.537	0.172	-8.925	<0.001	
Goniastrea pectinata	*c*	-1.158	0.435	-2.663	0.009	0.747
	m	-0.869	0.198	-4.394	<0.001	

299 Figure 1



300

301

302